

FORENSIC ENTOMOLOGY IN CRIMINAL INVESTIGATIONS

E. P. Catts

Department of Entomology, Washington State University, Pullman, Washington
99164-6432

M. L. Goff

Department of Entomology, University of Hawaii, Honolulu, Hawaii 96822

KEY WORDS: necrophages, postmortem interval, blow flies, corpse decomposition

PERSPECTIVES AND OVERVIEW

Forensic entomology is the application of the study of insects and other arthropods to legal issues, especially in a court of law. The past decade has seen a resurgence of interest in forensic investigations by entomologists. Lord & Stevenson (83) identified three categories of forensic entomology: urban, stored-product, and medicolegal. Urban forensic entomology includes such things as litigations and civil law actions involving arthropods in dwellings or as house and garden pests. Law suits dealing with the misuse of pesticides are included here. Stored-product forensic entomology generally deals with arthropod infestation or contamination of a wide range of commercial products (e.g. beetles or their parts in candy bars, flies in ketchup, or spiders in bathroom tissue). Like its urban counterpart, this category usually involves litigation. The third category, medicolegal forensic entomology, is the focus of this review and is the most popularized aspect of the science. It deals with arthropod involvement in events surrounding felonies, usually violent crimes such as murder, suicide, and rape, but also includes other violations such as physical abuse and contraband trafficking (116). A more accurate name for this category is medicocriminal forensic entomology (53).

The most common application of the medicocriminal category relates to death investigations. Key elements in these investigations, such as time since death (i.e. the time between death and corpse discovery, which is generally referred to as the postmortem interval or PMI), movement of the corpse, manner and cause of death, and association of suspects with the death scene, may all relate to arthropod occurrence and activities.

In an earlier review of forensic entomology, Keh (70) observed that accounts of the early use of entomology in criminal investigations are scarce. The earliest record of its use is Sung Tzu's 1235 AD discussion in a book entitled *The Washing Away of Wrongs* (91). In it he described the investigation of a homicide in which flies landing on a sickle indicated the murder weapon and resulted in a confession by the murderer. Forensic entomology in Europe began about a century ago with the work of Bergeret, Brouardel & Yovanovitch (70). This work was expanded by Megnin (93, 94), who carefully detailed the predictable succession of arthropods associated with a decomposing corpse. The first case study of forensic entomology in Europe was of the acquittal of a French couple of the death of an infant whose mummified remains and associated fauna were discovered behind the mantelpiece in their home (5).

Smith (116) notes that in the century since Megnin's research few forensically related works have appeared in entomological publications (120). However, if we include studies of carrion-frequenting species and the ecology of carrion decomposition, we find a sizable representation of about 400 papers focused on arthropods often associated with corpses. Some of these describe the character of the carrion community (22, 79, 106). Others treat the succession of this community (9, 19–21, 28, 67, 73, 96, 104, 118), and many deal with the biology of the arthropods (especially blow flies, beetles, and mites) most often associated with the decomposing corpse (60, 84, 107, 108).

Like Megnin, several workers have done much to advocate and legitimize the application of entomology to death investigation as it is perceived by law enforcement agencies (7, 25, 41, 47, 74, 109). To date, two books deal specifically with forensic entomology: the first (116) is directed mostly at entomologists, and the second (16) attempts to familiarize death investigators as well as entomologists with procedures and analysis in handling entomological data in death investigations.

Since the review by Keh (70), several areas of forensic entomology have progressed considerably. Some of these were reviewed recently by Leclercq & Brahy (75) along with an account of the history of forensic entomology. Here, we aim to identify the various applications of entomology to medicolegal situations and to highlight those approaches that have emerged during the past decade.

WHY USE INSECTS IN MEDICOCRIMINAL INVESTIGATIONS

There are several reasons for using insects in death investigations. First, insects are usually the first to find a decomposing corpse. Often blow flies, if given access, will oviposit on carrion within the first few hours following death (15). This action starts a biological clock whereby subsequent determination of the age of the developing fly progeny is the basis for estimating the PMI. Second, the arthropod fauna in and around a corpse changes in a rather predictable successional sequence as decomposition progresses. The corpse, a temporary resource, is exploited by a wide diversity of organisms ranging from microbes to vertebrate scavengers. Arthropods usually constitute the major element of this fauna, and insects predominate as the most constant, diverse, and conspicuous group present except in marine situations, where Crustacea predominate. In studies in South Carolina, 522 species of animals in 3 phyla were recovered from rotting fetal pig carcasses; 84% of these were insects (104). Similar studies in the Hawaiian Islands reported 140 arthropod taxa with a comparable 83% insects (39). Third, the corpse fauna often is ignored when investigators process the death scene (57). Often arthropods in the immediate vicinity of the corpse are overlooked as evidence. For example, in the seepage zone beneath the corpse, a complex community of mites (33) and insects may develop and will be lost as evidence in cases where specimens are collected only from the corpse either at the death scene or at autopsy (16).

The ecological roles of these arthropods may be put into four categories:

1. Necrophages—the species feeding on corpse tissue. They include Diptera (especially calliphorids and sarcophagids) and Coleoptera (silphids and dermestids). Age determination of these insects usually is the basis for making PMI estimations (13, 86, 97).
2. Omnivores—species such as ants, wasps, and some beetles that feed on both the corpse and associated fauna. Large populations of these species may retard the rate of corpse decomposition by depleting populations of necrophagous species (21).
3. Parasites and Predators—Smith (116) identified this group of arthropods as second to the necrophages in importance. Included here are many Coleoptera (silphids, staphylinids, histerids), Diptera (calliphorids), and those Hymenoptera that parasitize immature flies. Some species that are necrophagous during their early larval development become predaceous during their later larval instars (45). The array of mites (macrochelids, parasitids, parholaspids, and uropodids) probably also belong in this category as predators of other mites, insects, and nematodes (33, 76).

4. Incidentals—arthropods that use the corpse as a concentrated resource extension of their normal habitat. Springtails, spiders, centipedes, pill bugs, and some mites (Acaridae, Lardoglyphidae, and Winterschmidtidae) belong to this group (33).

ESTIMATING THE PMI

One can use entomological data to estimate the PMI in two basic ways. During the earlier progress of decomposition, the estimate is based on the time period needed for each represented species to develop to the growth form collected at the death scene. Most often these are fly maggots, primarily blow flies and flesh flies. Those showing the longest period of development are assumed to manifest the PMI provided the corpse was exposed and conditions were suitable for insect activity at the beginning of the period (13). Note that the key assumption made is that insects, usually flies, will discover the corpse soon after death or time of corpse exposure (15, 53). Sometimes this assumption is specious, and it must be evaluated carefully in estimating the PMI (13). This is especially true for indoor and closed-container death scenes, or where weather conditions are extreme.

The second basic approach to determining the PMI relates to those corpses in advanced stages of decomposition. PMI estimates in these cases are based on the composition of the arthropod community as it relates to expected successional patterns (40). Since the review by Keh (70), important advances in our understanding and application of both approaches have been made.

DIPTERAN BIOLOGY

Species Identification

One problem facing the entomologist is the accurate identification of the maggots collected from a corpse. All too frequently only dead specimens, often poorly preserved, are submitted for identification. Even when the local fauna is well known, identification can be difficult, particularly of the early-instar maggots. Work by Erzincioğlu (24) in England and by Liu & Greenberg (77) in the US have resulted in identification keys to eggs and larvae of some forensically important species. Haskell et al (56) and Hawley et al (58) have described situations in which identification of the larvae of aquatic Diptera on corpses has presented problems. Aquatic fresh water and marine fauna associated with submerged and floating corpses needs more emphasis in future studies. Recent advances that allow DNA probe identification of insects or their isolated body fragments, either fresh or dried, might be applicable to discriminating among species of maggots where morphological distinctions are lacking (66).

Age Determination of Maggots

Estimating the age of maggots collected from the corpse is a key element in analyzing insect fauna (13, 116). Over thirty years ago, Kamal (69) tabulated the development times for stages and instars of 13 species of carrion-frequenting blow flies and flesh flies in Washington. These studies were carried out in an air-conditioned insectary under nearly constant conditions. His results have become the baseline data often used to estimate the age of maggots by interpolating these data against on-site conditions. Unfortunately, some simple errors in summing the total development times were made in that publication. These inaccuracies have been reprinted in other works (116). In addition, the temperature at which Kamal's studies were done is misprinted as 22°C instead of 27°C. Most workers favor the use of their own locally generated development-rate data, but the risk of using inaccurate published data in making a PMI estimate remains.

Recently others have begun to repeat and refine this important baseline information, emphasizing the determination of temperature-induced variation in maggot development rates and sizes. Nishida and coworkers (98, 99) developed exact growth tables for seven species of blow flies and flesh flies. Vinogradova & Marchenko (121) presented threshold developmental temperatures for nine species of flies. Introna et al (61, 62) reared flies in a programmable growth chamber and were able to recreate closely the changing heat and light cycles of a field situation.

Summing of heat values as accumulated degree hours (ADH) for making time-line estimates has been discussed and illustrated by Greenberg (47) and Lord et al (80). They describe cases where ambient temperature data from weather stations located in the vicinity of the corpse were used to approximate hourly changes at the death scene. Lord and coworkers (81; W. D. Lord & T. R. Atkins, unpublished case study) demonstrated the value of using ADH estimates in situations where faunal populations are small, weather extreme, and multiple species present. However, except for indoor situations, reliance on ADH estimations can give a false perception of accuracy (13, 15). Introna et al (64) reared flies in screen-topped glass jars in the field during spring and summer to develop a local baseline development table. As expected, their data disagree with those based on the constant conditions used by Kamal (69), but their methods fail to indicate the size of the fly populations relative to the amount of feeding substrate, and their temperature data are summarized. However, ADH calculations can be valuable when the heating or cooling regimen can be determined. The need for very careful experimental design and data recording in establishing baseline data on fly development cannot be overemphasized. Eventually, computer modeling of maggot development may refine the accuracy of estimating maggot age. Toward this end, Williams

(124) developed and tested a model for determining the time of blow fly egg hatch based on maggot weight and temperature record.

An accurate record of ambient conditions during the postmortem interval is a key element in determining the age of associated maggots. Generally, airfield weather stations provide the most detailed record of conditions, but rarely is a weather station close to the death scene. Haskell & Williams (57) recommend the recording of ambient conditions at the death scene for 3–5 days following corpse discovery and removal. This record then can be compared with that of the more distant station and consistent differences taken into account in attempting to describe previous on-site conditions.

Another important consideration related to maggot development rates is the amount of metabolic heat generated by the maggots massed in the corpse (15, 90). Ambient temperatures often do not reflect those to which maggots are exposed. Payne (104) noted that carcass temperatures often are elevated, and Early & Goff (21) and Tullis & Goff (118) recorded internal carcass temperatures as much as 22°C above ambient in the mild climate of Hawaii. The development of this endothermic system in carrion was studied by Cianci & Sheldon (17). They described a delayed onset of heat production and the importance of corpse shading and sun exposure. Catts (15) discussed the influence of maggot-generated heat on corpse-community development and on subsequent analysis of entomological data. The stabilizing effect of maggot mass-generated heat was studied in human remains by Marchenko & Vinogradova (90) in the USSR. Laboratory studies by Goodbrod & Goff (45) demonstrated that massed maggots heated their substrate at population densities as low as four larvae per gram of medium. Marchenko (88, 89) determined a lower density threshold for maggot-generated heat to be a 1:1 ratio of maggot to grams of medium but that at a 2:1 ratio “considerable accelerated” development occurred (88). Because maggots aggregate within the corpse, a high density of maggots regularly occurs in spaces unaffected by daily swings in temperature (87).

The level of generated heat also can selectively affect the species of maggots represented. Williams & Richardson (125) noted that higher temperatures of a mixed-species maggot mass were tolerated by *Chrysomya rufifacies*, but that populations of *Lucilia cuprina* were “burned out.” Thus, the effect of maggot-generated heat can influence: (a) the rate of maggot development, (b) the development of subcorpse fauna, (c) the character of the corpse community, (d) the validity of ADH calculations, and (e) the effect of refrigeration of the corpse prior to autopsy (15).

Age Determination of Puparia and Adult Flies

Recently, attention has focused on the age determination of puparia and adult flies (13, 48, 100, 110). Greenberg points out that because as much as 40% of

the blow fly life span is spent as a puparium, valuable time-line evidence can be gained by aging this stage in detail. He has initiated studies of the chronological changes occurring on the surface of the pupa within the puparium and of the dispersal distances traveled by postfeeding maggots prior to pupariation.

The age determination of adult flies also can have forensic implications, especially in indoor death-scene investigations. Living and dead adult flies attracted to or produced from a corpse usually occur in considerable numbers inside windows following their emergence. Investigators have aged adults by analyzing the pteridine levels in the eyes of adult screw-worm flies (117, 122). Pteridine is sequestered as a stored excretion in the eyes and can be measured with a high degree of accuracy in fresh or dried specimens. Another method is the counting of cuticular bands added daily to the skeletal apodemes of blow flies (119).

Species Invasions, Patchy Distribution, and Biological Variation

Four recently introduced species of *Chrysomya* considered to be of forensic as well as medical importance have been found in the Americas within the past decade (49). Of these, *C. megacephala* and *C. rufifacies* were reported previously from Hawaii where they occur in association with carrion and corpses (39, 41, 42, 44). The northward advance of these species along with *C. albiceps* and *C. putoria* has been well documented (1, 3, 4, 29). Studies of the interaction of *C. rufifacies* with maggots of other blow fly species have demonstrated the dominance of this species in several ways: toleration of higher substrate temperatures (125), toleration of higher maggot densities (45), and a transition to predator status in crowded populations (45). In South Africa, two species of *Chrysomya* were the major determinants of carrion community structure in dead impalas (11). These species, *C. albiceps* and *C. marginalis*, showed dispersal rates of 2.20 and 2.34 km/day, respectively (12).

Seasonal sampling of blow flies shows distinct variations in the mix of species in Illinois (2), Mississippi (32), and Maryland (63). In England during winter periods, trichocerid gnats replaced blow flies as the initial arrivals at carrion (23). These gnats also were reported from a corpse in Ohio (W. D. Lord & N. H. Haskell, unpublished case study).

Spatial dispersion of blow flies also varies considerably and has little relationship to the composition of the maggot community in carrion (54). Hanski (55) reported strong local variations in species at carrion and concluded that this diversity results from local environmental variations as yet unstudied. Blackith & Blackith (8) found that the mix of fly species at small carrion was different from what was anticipated based on background sam-

pling. Blow fly numbers were extremely incongruous in traps only 100 m apart. In any case, background surveys should employ a variety of sampling methods to assure validity (20).

There is growing concern that the biology of blow fly species with very wide geographic distributions have some forensically important intraspecific variations (15, 116). Although the black blow fly, *Phormia regina*, was described in Texas as inactive during the summer, it is an early and ubiquitous carrion breeder throughout the summer in the northern US (N. H. Haskell, unpublished data). In addition, where *Calliphora vomitoria* was once considered rare in the US, it is now fairly common during cool spring and fall periods (E. P. Catts & N. H. Haskell, unpublished data). Greenberg (50) demonstrated the readiness of *Phaenicia sericata* to oviposit under uncharacteristic cool nocturnal conditions. These differences may reflect unstudied areas of blow fly behavior, intraspecific racial variations, or microclimatic differences.

Delayed Corpse Invasion

Circumstances surrounding the death scenario can profoundly affect the time of initial appearance of insects at a corpse. In a couple of recently described homicide investigations, blow fly invasion of the corpse was delayed for several days because the corpse had been wrapped in several layers of blankets (26, 36). In the first case, entry was delayed even though the corpse had been exposed for four days prior to concealment. In the second, investigators subsequently simulated the homicide scenario by substituting a pig for the corpse in order to determine the presumed delay in fly invasion (36).

In Louisiana, studies are in progress to determine the time delay preceding blow fly strike on bodies inside of a closed automobile trunk compartment. Preliminary results (1990) showed a delay of three days for pig carrion in the trunk during the fall season (L. Meek, unpublished data). These studies also involve the delay of fly invasion on burned flesh. Burning and charring of flesh appears to retard its immediate attractiveness to blow fly strike. Approximately a one-week delay in fly strike occurred on pig carrion contained inside an automobile that was set afire (L. Meek, unpublished data). However, in a homicide case involving a corpse that had been burned and charred inside of an open-topped metal drum, abundant fly strike occurred within a few days of death (N. H. Haskell, unpublished data). A plethora of reasons might account for these differences, but we must wait for the completion of this research before suggesting the cause. It is sufficient to conclude that fly strike on a corpse is not always immediate.

CORPSE DECOMPOSITION

The process of corpse decomposition is basic to the use of entomology for estimating the PMI in death investigations. Information of value to entomology may be gleaned from recent studies in forensic anthropology even though most of these do not deal with the associated arthropod fauna. The opportunity to use human remains for such studies are rare (111, 115). At the Anthropological Research Facility (ARF) in Tennessee, Rodriguez & Bass (111) described patterns of corpse decomposition as related to insect activity. Although this research was done under atypical conditions (corpses enclosed in a wire cloth coffin were suspended above a concrete slab substrate), the insect activity patterns do agree very closely with those from nonhuman carrion (104). Later, Rodriguez & Bass (112) expanded their research at the ARF to include the decomposition of buried corpses under conditions that simulated those of a burial death scene. Studies of the decay rates of 150 corpses at the woodland ARF in eastern Tennessee (85) indicated the three most important environmental factors in corpse decay: temperature, access by insects, and depth of burial. Gaping wounds or stabbing also increased the rate of decomposition. However, these authors' conclusion that blow flies typically arrive within a few seconds following corpse exposure must be viewed with reference to the ARF study site, where for years numerous human remains have been exposed continuously, and local populations of carrion insects are concentrated and abundant.

One area of frequent concern regarding the validity of baseline data obtained from decomposition studies is the kind of nonhuman model used. A wide array of different animals are used in decomposition studies ranging from lizards and toads (19), to mice and birds (8), to cats and pigs (21, 59) and even elephants (18). The validity of extrapolating from these studies to human corpses has been questioned in court trial cases. The animal model must (*a*) closely approximate the pattern of human corpse decomposition, (*b*) be relatively easy to obtain, (*c*) be inexpensive, and (*d*) not tend to arouse public objections. The domestic pig appears to be the most acceptable animal as a model, and it has been used frequently in recent decomposition studies. The recommended size of pig is about 23 kg, with some latitude. Hewadikaram & Goff (59) showed that patterns of arthropod succession did not differ significantly between pig carcasses that had moderate weight differences. Extreme differences in corpse size, however, greatly affect the rate of decomposition (73). In 1989, N. H. Haskell (unpublished data), working at the ARF, compared the community structure and rates of decomposition between adult and infant human remains and the pig model. The communities did not differ, but the rate of decomposition was governed by the amount of carrion

available. The infant corpse decomposed to skeletal remains in 5 days while the adult human and pig required 3 to 5 times as long. Comparisons of rates of decomposition among the remains of dogs, cats, and humans have been made in an arid environment, but the insect fauna was not treated in detail (30).

Disturbance of the carrion mass can affect the rate of decomposition (15, 21, 59). Such disturbance can occur either in controlled studies by the investigator (59) or at the death scene where large scavengers drag or disarticulate the corpse (52).

In addition to the choice of a suitable nonhuman animal model, the researcher must consider the condition of the carcass studied. Several studies used carcasses that were frozen and thawed prior to exposure, but Micozzi (95) has demonstrated differences in the character of decomposition between fresh and thawed carcasses. Frozen-thawed carcasses showed predominantly aerobic decomposition in the field whereas fresh carcasses showed anaerobic putrefaction. Also, decomposition of thawed corpses in northern latitudes is accelerated following prolonged freezing exposure (13).

Arthropod succession in decomposing carcasses has been studied in different parts of the world. More analyses have been conducted in temperate regions (8, 9, 28, 31, 67, 104, 106) and fewer in the tropics (10, 11, 21, 65, 118). Successional studies in arid climes appear to be rare (30, 113). A common format for most of these studies has been an attempt to subdivide the overall decomposition process into a chain of integrated stages, each with characteristic appearance, physical parameters, and assemblage of arthropods. Schoenly & Reid (114) emphasized that such subdivisions are quite artificial and that specific combinations of physical characteristics and arthropod assemblages do not exist in nature. Even so, these descriptive stages are valuable as a time-line reference in the decomposition process. This value is particularly apparent when, as an expert witness, the forensic scientist must explain events associated with corpse decomposition to a jury.

Regardless of the locality, certain patterns are common to most, if not all, decomposition studies. The duration of each stage, or phase, of decomposition may differ, but the order of occurrence is constant. Although the faunas involved are parochial in species, the same taxonomic families are usually present. The decomposition process is generally subdivided into five stages: fresh, bloat, active decay, post or advanced decay, and dry or skeletal remains (21, 118). The overall process can be viewed as a two-act play with an intermission between acts (15). The first act includes the first three stages of decomposition and is an accelerated performance in which maggots take top billing. The intermission is marked by a rapid decrease in corpse biomass resulting from loss of seepage fluids and dispersal of postfeeding maggots. The second act is comprised of the last two stages of decomposition and is prolonged in duration.

DETECTION OF ANTEMORTEM DRUGS AND TOXINS

Beginning with the work of Nuorteva (102, 103) interest has increased in the potential use of insects for detecting certain substances in decomposing tissues. Beyer et al (6) detailed a suicide case where analysis of maggots infesting the well-decomposed corpse showed traces of phenobarbitol. Introna et al (63) showed that opiates could be detected by analyzing maggots and suggested that quantitative relationships may be of value. Kintz et al (71) demonstrated that triazolam, oxazepam, alimemazine, and chloripriamine in addition to phenobarbitol could be detected in maggots that had developed in a corpse. Gunatilake & Goff (51) detected the organophosphate malathion in blow fly maggots feeding on a corpse in a case of suicide. Here, the concentration of toxin in *Chrysomya* species was 2050 $\mu\text{g/g}$.

These studies have focused on the detection of drugs or toxins through the analysis of maggots that had fed on intoxicated tissues. Little attention has been given to the effects of these substances, or their metabolites, on the developing maggots. Goff et al (43) investigated the effect of cocaine and its metabolite benzoylecognine on the rate of development of a sarcophagid, *Boettcherisca peregrina*. Lethal doses of cocaine in decomposing rabbit tissue significantly accelerated the growth rate of maggots feeding on the tissue. No differences were observed in either the duration of pupariation or adult fecundity. Lord (78) detailed two cases involving drugs. One was a death caused by drug overdose in which traces of cocaine were recovered from maggots in the corpse. The other was a cocaine-related homicide in which the growth rate of some of the associated maggots appeared to have been accelerated. Similar studies (37) on the effect of heroin also showed accelerated maggot growth. Furthermore, the amount of heroin (as morphine) present in tissues and the duration of pupariation were directly related. Again, adult flies exhibited no detectable effects. Current research involves the effect of methamphetamines on maggot development. Recent studies unrelated to carrion decomposition suggest that corpse fauna that feed on maggots also may be analyzed for drugs (27). This work has demonstrated strong similarity in the cuticular surface chemistry for species interacting at four different trophic levels. There is a need for additional research and for caution in interpretations of data from death investigations that possibly involve the use of drugs.

APPLICATIONS TO FORENSIC PROBLEMS

The preceding sections have detailed some of the recent advances in biology of Diptera, determinations of baseline data for local faunas, and effects of drugs and toxins in tissues on developmental rates. These data are all neces-

sary preliminaries to the actual process of estimating a postmortem interval but, by themselves, will not provide the estimate. Not all types of data are significant for all cases. In processing the data and developing the PMI estimate, the entomologist must bear in mind that the estimate is of duration of arthropod activity and not necessarily of the total postmortem interval. Erzinclioglu (25) stated that each case must be taken on its own merits and that no general rules for procedure can be laid down. We agree that each case is unique, but argue that some general rules should be laid down for dealing with entomological evidence. The entomologist must select the appropriate data sets and apply them carefully to each case. As noted earlier during discussions of decomposition, the populations of insects that may be associated with a corpse vary geographically and seasonally. Even in cases where the species compositions are similar, seasonally induced differences in developmental patterns may complicate analyses. Given the bulk of data available from the various sources, computers may become a major aid in selection and processing of the appropriate data (40, 41). Computer programs and data bases are being independently compiled by several different forensic entomology programs, and the eventual combination of these data bases and programs into a centralized data base should be seriously considered.

In addition to the gathering and processing of entomological data, the forensic entomologist must develop a workable protocol for cooperation with various law-enforcement agencies, coroners, and medical examiners. Several workers have formulated their own protocols for collecting and processing entomological evidence. Lord & Burger (79) provided instructions dealing with collection of insects and other arthropods from corpses. This paper was primarily oriented toward the nonentomologists such as the police and crime-scene technicians who would be involved in crime-scene processing. Meek et al (92) provided suggested procedures for entomologists when collecting at the crime scene. Smith (116) also suggested guidelines for collection of arthropods and subsequent handling of the specimens. Haskell (57) developed a detailed checklist for death-scene and autopsy entomologists and nonentomologists in the publication entitled *Entomology and Death: a Procedural Guide* (16). However, each jurisdiction may have its own requirements, and procedures can vary accordingly.

The level of interaction between the forensic entomologist and the various agencies involved in criminal investigation also varies. In a few jurisdictions, the entomologist may become a routine part of the homicide investigation team, being notified whenever decomposing remains are found and beginning investigations while the corpse is still at the site. In most other areas, this is not practical, and the entomologist often is provided only with specimens collected from the corpse at autopsy.

Useful faunal data can be lost, ignored, or even destroyed at the death scene

when investigators lack training in what to look for and how to collect and preserve it (79). Every forensic entomologist can help solve this problem by teaching death-scene investigators how to collect specimens and other related on-site data by conducting workshops and training programs.

In addition to the data bases and protocols currently available, the case studies that have been published are quite valuable. These provide examples of applications of the various approaches for determination of PMI estimates and other types of forensic problems. Smith (116) has provided a series of 19 cases in his textbook, beginning with that of Bergeret in 1850 and other cases submitted by European forensic entomologists, including A. M. Easton & K. V. G. Smith, M. Leclercq, and P. Nuorteva.

Lord (78) detailed 26 cases and grouped them according to the fauna involved. Greenberg (47) also provides an account of several case studies from his work, giving particular emphasis to temperature-related variations and concerns. Lord et al (80, 81) present cases in which the estimates of postmortem interval are based primarily on the developmental periods of a single fly species and are dependent on an accumulated degree hour extrapolation. In a publication aimed primarily at the legal profession, Lord & Rodriguez (82) presented discussions of techniques along with selected applications to case studies. Goff et al (40, 41, 44) present case studies in a tropical setting during the later stages of decomposition where the interpretations depend more on comparisons of arthropod succession patterns determined from baseline decomposition studies. Kulshrestha & Chandra (72) discuss their work in India primarily with respect to observations of insects on corpses and results of their laboratory studies. Marchenko (86) and Nainis et al (97) present case studies from the USSR in considerable detail, with special attention to temperature-induced variations in rates of development. The paper by Nuorteva (100) dealing with the use of empty puparia in Finland to determine season of death, rather than to estimate the postmortem interval, is of special interest as this aspect is often overlooked by crime-scene investigators. Leclercq & Verstraeten (76) provide data concerning the presence of mites on decomposing remains, and Goff (35) documents the application of acarological data to estimations of postmortem intervals in a case of a burial on the island of Oahu, Hawaii. Discussions of potential uses of aquatic insects in determination of the interval of submersion of a corpse are presented by Haskell et al (56), followed by the presentation of two cases involving chironomid larvae by Hawley et al (58). Interestingly, the larvae in these cases were initially identified as "fibers" by the nonentomologist involved. This observation serves to emphasize the need for training death-scene investigators to recognize the fauna characteristic of a given site.

Differences in the geographic and habitat distributions of the various taxa involved in decomposition are well illustrated by even a casual examination of

case studies. These differences may indicate movement of a corpse from an urban to a rural habitat. Presence of species typically associated with one type of habitat on a corpse found in a different habitat should alert the forensic entomologist to the possibility that the corpse was transported following death. In like manner, an obvious gap in the pattern of larval development for Diptera species may indicate transport of the corpse (M. L. Goff, unpublished case data). In one comparison, insects recovered from 35 corpses had similar confirmed postmortem intervals (34). These corpses were recovered from both outdoor and indoor situations. Of the taxa recovered, only 23% were common to both types of habitats; the remainder was indicative of either indoor or outdoor disposal of corpses. Predictably, greater numbers of both species and individual insects were associated with corpses outdoors.

While most publications noted above emphasize the estimation of postmortem intervals, the potential for use of entomological evidence in cases involving living individuals also has been documented. In California, Webb et al (123) were able to determine that a suspect had been at the scene of a homicide because of observation of bites of the chigger *Eutrombicula belkini* on both the suspect and on death-scene investigators. Prichard et al (105) further discussed the dermatological aspects of this case. Lord & Rodriguez (82) described the use of entomological evidence in a case of child neglect. In that case, the duration of the neglect was determined by development of maggots in diapers. More recently, Goff et al (38) detailed the use of maggot development of *Chrysomya megacephala* to determine a period of exposure for a case of child abuse/attempted murder. In this case, the maggots were developing in fecal material inside of a disposable diaper on a 16-month-old child abandoned at the edge of a lake. In addition to feeding on the fecal material, the maggots had also invaded the genital and rectal areas and were feeding on living tissues. Grace et al (46) reported that ABO blood typing of human saliva samples taken from the surface of a corpse in Los Angeles was not affected by the trail-marking contamination of the Argentine ant, *Iridomyrmex humilis*.

CURRENT PERCEPTIONS OF FORENSIC ENTOMOLOGY

The increased level of awareness of forensic research within the entomological community is evidenced by the packed-house symposia presented at annual meetings of the Entomological Society of America, 1984 and 1990, the symposium presented during the 18th International Congress of Entomology in 1988, and the sessions in forensic entomology during the 2nd International Congress of Dipterology, 1990. Researchers in related disciplines

are also more aware of the use of entomological evidence. The National Association of Medical Examiners presented a symposium on forensic entomology during their annual meeting in 1985. Since 1989, the American Academy of Forensic Sciences has sponsored workshops on the evidence and recovery of decomposed corpses in which presentations of forensic entomology have been a major component. A similar workshop was held during the 14th International Academy of Legal and Social Medicine during 1988, and sessions were included in the 12th International Meeting of Forensic Sciences, 1990. The uses of Diptera larvae in detection of drugs and toxins were discussed at the International Symposium on the Forensic Aspects of Mass Disasters and Crime Scene Reconstruction held by the US Federal Bureau of Investigation in 1990. Apart from this level of interest, the actual levels of cooperation and understanding between forensic entomologists and death-investigation workers vary considerably. Some forensic entomology programs enjoy a high level of cooperation with law-enforcement agents, while others are largely excluded from investigations. One major problem hindering uniform acceptance of techniques of forensic entomology may lie in the do-it-yourself nature of the programs currently operating. To a large extent, an entomologist wishing to establish a program in forensic entomology must provide his own education in the specialty and then convince both the law-enforcement agencies and the judicial system of his/her competence in the field. At present, no formal training programs are available for entomologists wishing to pursue this avenue of investigation, and no agencies currently provide any form of certification. This situation presents difficulties when the entomologist attempts to interact with disciplines, such as law enforcement and medicine, where considerable emphasis is placed on board certifications and documented workshop attendance for continuing education. Some form of certification for forensic entomologists including a code of ethics (14) and a specified curriculum training program should be established to reinforce the credibility and protect the integrity of the discipline. This concept is well expressed by Greenberg (48) in his review of Smith's text (116): "'Mathematics for the million' is fine, but maggots for the million won't hold up in court."

For the general public, forensic entomology apparently exerts an attraction-repulsion effect. Recently, several popular science journals produced articles dealing with forensic entomology. These articles, to date, have been well written and provide the public with readable accounts of the field without undue emphasis on the less aesthetically pleasing aspects (25, 68). The use of insects in homicide investigations was recently highlighted in a major motion picture, *Silence of the Lambs*. At the present time, public perception of forensic entomology appears to be positive, although relatively few people appear to wish a close encounter with the subject.

Literature Cited

1. Baumgartner, D. L. 1986. The hairy maggot blow fly *Chrysomya rufifacies* (Macquart) confirmed in Arizona. *J. Entomol. Sci.* 21:130-32
2. Baumgartner, D. L. 1988. Spring season survey of the urban blowflies (Diptera: Calliphoridae) of Chicago, Illinois. *Great Lakes Entomol.* 21:119-21
3. Baumgartner, D. L., Greenberg, B. 1984. The genus *Chrysomya* (Diptera: Calliphoridae) in the New World. *J. Med. Entomol.* 21:105-13
4. Baumgartner, D. L., Greenberg, B. 1985. Distribution and medical ecology of the blow flies (Diptera: Calliphoridae) of Peru. *Ann. Entomol. Soc. Am.* 78: 565-87
5. Bergeret, M. 1855. Infanticide, momification du cadavre. Decouverte du cadavre d'un enfant nouveau-ne dans une cheminee ou il s'etait momifie. Determination de l'epoque de la naissance par la presence de nymphes et de larves d'insectes dans le cadavre et par l'etude de leurs metamorphoses. *Ann. Hyg. Publique Med. Leg.* 4:442-52
6. Beyer, J. C., Enos, W. F., Stajic, M. 1980. Drug identification through analysis of maggots. *J. Forensic Sci.* 25:411-12
7. Bianchini, G. 1930. La biologia del cadavere. *Arch. Antropol. Crim. Psychiatr. Med. Leg.* 50:1035-105
8. Blackith, R. E., Blackith, R. M. 1990. Insect infestations of small corpses. *J. Nat. Hist.* 24:699-709
9. Bornemissza, G. F. 1957. An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. *Aust. J. Zool.* 5:1-12
10. Braack, L. E. O. 1981. Visitation patterns of principal species of the insect-complex at carcasses in the Kruger National Park. *Koedoe* 24:33-49
11. Braack, L. E. O. 1986. Arthropods associated with carcasses in the Northern Kruger National Park. *S. Afr. J. Wildl. Res.* 16:91-98
12. Braack, L. E. O., Retief, P. F. 1986. Dispersal, density and habitat preference of the blow-flies *Chrysomya albiceps* (WD) and *Chrysomya marginalis* (WD) (Diptera: Calliphoridae). *Önderstepoort J. Vet. Res.* 53:13-18
13. Catts, E. P. 1991. Analyzing entomological data. See Ref. 16, pp. 24-35
14. Catts, E. P. 1991. Report/witness ethics. See Ref. 16, pp. 150-53
15. Catts, E. P. 1992. Problems in estimating the PMI in death investigations. *J. Agric. Entomol.* In press
16. Catts, E. P., Haskell, N. H., eds. 1991. *Entomology and Death: a Procedural Guide*. Clemson, SC: Joyce's Print Shop. 180 pp.
17. Cianci, T. J., Sheldon, J. K. 1991. The creation of an endothermic system by the larvae of the blowfly *Phormia regina* Meigen developing in pig carcasses. *J. Soc. Vector Ecol.* In press
18. Coe, M. 1978. The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya. *J. Arid Environ.* 1:71-86
19. Cornaby, B. W. 1974. Carrion reduction by animals in contrasting tropical habitats. *Biotropica* 6:51-63
20. Disney, R. H., Erzincioğlu, Y. Z., Henshaw, D. J. deC., House, D., Unwin, D. M., et al. 1982. Collecting methods and the adequacy of attempting fauna surveys, with reference to the diptera. *Field Stud.* 5:607-21
21. Early, M., Goff, M. L. 1986. Arthropod succession patterns in exposed carrion on the island of O'ahu, Hawaiian Islands, USA. *J. Med. Entomol.* 23:520-31
22. Easton, A. M., Smith, K. V. G. 1970. The entomology of the cadaver. *Med. Sci. Law* 10:208-15
23. Erzincioğlu, Y. Z. 1980. On the role of *Trichocera* larvae (Diptera, Trichoceridae) in decomposing carrion in winter. *Naturalist* 105:133-34
24. Erzincioğlu, Y. Z. 1985. Immature stages of British *Calliphora* and *Cynomya*, with a re-evaluation of the taxonomic characters of larval Calliphoridae (Diptera). *J. Nat. Hist.* 19:69-96
25. Erzincioğlu, Y. Z. 1985. Few flies on forensic entomologists. *New Sci.* May 1985:15-17
26. Erzincioğlu, Y. Z. 1985. The entomological investigation of a concealed corpse. *Med. Sci. Law* 25:228-30
27. Espelle, K. E., Brown, J. J. 1990. Cuticular hydrocarbons of species which interact on four trophic levels: apple, *Malus pumila* Mill.; codling moth, *Cydia pomonella* L., a hymenopteran parasitoid, *Ascogaster quadridentata* Wesm.; and a hyperparasite, *Perilampus fulvicornis* Ashmead. *Comp. Biochem. Physiol.* 95B:131-36
28. Fuller, M. E. 1934. The insect inhabitants of carrion, a study in animal ecology. *Bull. Aust. Counc. Sci. Ind. Res.* 82:1-62
29. Gagne, R. J. 1981. *Chrysomya* spp., Old World blow flies (Diptera: Cal-

- liphoridae), recently established in the Americas. *Entomol. Soc. Am. Bull.* 27:21-22
30. Galloway, A., Birkby, W. H., Jones, A. M., Henry, T. E., Parks, B. O. 1989. Decay rates of human remains in an arid environment. *J. Forensic Sci.* 34:607-16
31. Giachino, P. M., Tosti-Croce, E. 1986. Note su alcune specie di *Catopidi* (Coleoptera, Catopidae) associate alla decomposizione di un cadavere di micro-mammifero. *Bull. Mus. Reg. Sci. Nat. Torino* 4:395-411
32. Goddard, J., Lago, P. K. 1985. Notes on blow fly (Diptera: Calliphoridae) succession on carrion in northern Mississippi. *J. Entomol. Sci.* 20:312-17
33. Goff, M. L. 1989. Gamasid mites as potential indicators of postmortem interval. In *Progress in Acarology*, ed. G. P. Channabasavanna, C. A. Viraktamath, 1:443-50. New Delhi: Oxford & IBH
34. Goff, M. L. 1991. Comparison of insect species associated with decomposing remains recovered inside of dwellings and outdoors on the island of Oahu. *J. Forensic Sci.* 36:748-53
35. Goff, M. L. 1991. Use of Acari in establishing a postmortem interval in a homicide case on the island of Oahu, Hawaii. *Proc. 8th Inter. Congr. Acarology, Ceske Budejovice, Aug. 1990*. Prague: Academia; the Hague: SBP Academic. In press
36. Goff, M. L. 1992. Problems in estimating the postmortem interval resulting from wrapping of the corpse: a case study from Hawaii. *J. Agr. Entomol.* In press
37. Goff, M. L., Brown, W. A., Hewadikaram, K. A., Omori, A. I. 1991. Effect of heroin in decomposing tissues on the development rate of *Boettcherisca peregrina* (Diptera: Sarcophagidae) and implications to the estimation of postmortem intervals using arthropod developmental patterns. *J. Forensic Sci.* 36:537-42
38. Goff, M. L., Charbonneau, S., Sullivan, W. 1991. Presence of fecal material in diapers as a potential source of error in estimations of postmortem interval using arthropod developmental rates. *J. Forensic Sci.* In press
39. Goff, M. L., Early, M., Odom, C. B., Tullis, K. 1986. A preliminary checklist of arthropods associated with exposed carrion in the Hawaiian Islands. *Proc. Hawaii. Entomol. Soc.* 26:53-57
40. Goff, M. L., Flynn, M. M. 1991. Determination of postmortem interval by arthropod succession: a case study from the Hawaiian Islands. *J. Forensic Sci.* 36:607-14
41. Goff, M. L., Odom, C. B. 1987. Forensic entomology in the Hawaiian Islands: three case studies. *Am. J. Forensic Med. Pathol.* 8:45-50
42. Goff, M. L., Odom, C. B., Early, M. 1986. Estimation of postmortem interval by entomological techniques: a case study from Oahu, Hawaii. *Bull. Soc. Vector Ecol.* 11:242-46
43. Goff, M. L., Omori, A. I., Goodbrod, J. R. 1989. Effect of cocaine in tissues on the development rate of *Boettcherisca peregrina* (Diptera: Sarcophagidae). *J. Med. Entomol.* 26:91-93
44. Goff, M. L., Omori, A. I., Gunatillake, K. 1988. Estimation of postmortem interval by arthropod succession: three case studies from the Hawaiian Islands. *Am. J. Forensic Med. Pathol.* 9:220-25
45. Goodbrod, J. R., Goff, M. L. 1990. Effects of larval population density on rates of development and interactions between two species of *Chrysomya* (Diptera: Calliphoridae) in laboratory culture. *J. Med. Entomol.* 27:338-43
46. Grace, J. K., Wood, D. L., Grunbaum, B. W. 1986. Effect of Argentine ant contamination on ABO blood typing of human saliva samples. *Bull. Entomol. Soc. Am.* 32:147-49
47. Greenberg, B. 1985. Forensic entomology: case studies. *Bull. Entomol. Soc. Am.* 31:25-28
48. Greenberg, B. 1988. A manual of forensic entomology (book review). *J. New York Entomol. Soc.* 96:489-91
49. Greenberg, B. 1988. *Chrysomya megachephala* (F.) (Diptera: Calliphoridae) collected in North America and notes on *Chrysomya* species present in the New World. *J. Med. Entomol.* 25:199-200
50. Greenberg, B. 1990. Nocturnal behavior of blow flies (Diptera: Calliphoridae). *J. Med. Entomol.* 27:807-10
51. Gunatillake, K., Goff, M. L. 1989. Detection of organophosphate poisoning in a putrefying body by analyzing arthropod larvae. *J. Forensic Sci.* 34:714-16
52. Haglund, W. D., Reay, D. T., Swindler, D. R. 1989. Canid scavenging/disarticulation sequence of human remains in the Pacific northwest. *J. Forensic Sci.* 34:587-606
53. Hall, R. D. 1991. Medicocriminal entomology. See Ref. 16, pp. 1-8
54. Hanski, I. 1976. Breeding experiments with carrion flies (Diptera) in natural conditions. *Ann. Entomol. Fenn.* 42: 113-21

55. Hanski, I. 1987. Carrion fly community dynamics: patchiness, seasonality and coexistence. *Ecol. Entomol.* 12:257-66
56. Haskell, N. H., McShaffrey, D. G., Hawley, D. A., Williams, R. E., Pless, J. E. 1989. Use of aquatic insects in determining submersion interval. *J. Forensic Sci.* 34:622-32
57. Haskell, N. H., Williams, R. E. 1991. Collection of entomological evidence at the death scene. See Ref. 16, pp. 82-96
58. Hawley, D. A., Haskell, N. H., McShaffrey, D. G., Williams, R. E., Pless, J. E. 1989. Identification of red "fiber": chironomid larvae. *J. Forensic Sci.* 34:617-21
59. Hewadikaram, K. A., Goff, M. L. 1991. Effect of carcass size on rate of decomposition and arthropod succession patterns. *Am. J. Forensic Med. Pathol.* In press
60. Hobson, R. P. 1932. Studies on the nutrition of blow-fly larvae. III. The liquification of muscle. *J. Exp. Biol.* 9:359-65
61. Introna, F., Altamura, B. M. 1988. Experimental reconstruction of *Calliphora erythrocephala* and *Lucilia sericata* life cycles in the growth cabinet. *Proc. XIV Congr. Inter. Acad. Legal Med. & Soc. Med., Liege.* Abstr.
62. Introna, F. Jr., Altamura, B. M., Dell'Erba, A., Dattoli, V. 1989. Time since death definition by experimental reproduction of *Lucilia sericata* cycles in growth cabinet. *J. Forensic Sci.* 34:478-80
63. Introna, F., Lo Dico, C., Caplan, Y. H., Smialek, J. E. 1990. Opiate analysis in cadaveric blowfly larvae as an indicator of narcotic intoxication. *J. Forensic Sci.* 35:118-22
64. Introna, F. Jr., Suman, T. W., Smialek, J. E. 1991. Sarcophagous fly activity in Maryland. *J. Forensic Sci.* 36:238-43
65. Jiron, L. F., Cartin, V. M. 1981. Insect succession in the decomposition of a mammal in Costa Rica. *J. New York Entomol. Soc.* 89:158-65
66. Johnson, D. W., Cockburn, A. F. 1992. Insect identification using DNA probes. *Arch. Biochem. Physiol.* In press
67. Johnson, M. D. 1975. Seasonal and microseral variation in the insect populations of carrion. *Am. Midl. Nat.* 93:79-90
68. Johnston, J. 1990. Entomology my dear Watson. *J. NIH Res.* 2:40
69. Kamal, A. S. 1958. Comparative study of thirteen species of sarcosaprophagous Calliphoridae and Sarcophagidae (Diptera). I. Bionomics. *Ann. Entomol. Soc. Am.* 51:261-70
70. Keh, B. 1985. Scope and applications of forensic entomology. *Annu. Rev. Entomol.* 30:137-54
71. Kintz, P., Godelar, B., Tracqui, A., Mangin, P., Lugnier, A. A., Chaumont, A. J. 1990. Fly larvae: a new toxicological method of investigation in forensic science. *J. Forensic Sci.* 35:204-7
72. Kulshrestha, P., Chandra, H. 1987. Time since deaths: an entomological study on corpses. *Am. J. Forensic Med. Pathol.* 8:233-38
73. Kuusela, S., Hanski, I. 1982. The structure of carrion fly communities: the size and type of carrion. *Holarctic Ecol.* 5:337-48
74. Leclercq, M. 1983. Entomologie et medecine legale; datation de la mort, observation indite. *Rev. Med. Liege* 38:735-38
75. Leclercq, M., Brahy, G. 1990. Entomologie et medecine legale: origines, evolution, actualisation. *Rev. Med. Liege* 45(7):348-58
76. Leclercq, M., Verstraeten, Ch. 1988. Entomologie et medecine legale. Datation de la mort. Acariens trouves sur des cadavres humains. *Bull. Ann. Soc. R. Belge Entomol.* 124:195-200
77. Liu, D., Greenberg, B. 1989. Immature stages of some flies of forensic importance. *Ann. Entomol. Soc. Am.* 82:80-93
78. Lord, W. D. 1991. Case histories of the use of insects in investigations. See Ref. 16, pp. 9-37
79. Lord, W. D., Burger, J. F. 1983. Collection and preservation of forensically important entomological materials. *J. Forensic Sci.* 28:936-44
80. Lord, W. D., Catts, E. P., Scarboro, D. A., Hadfield, D. B. 1986. The green blow fly, *Lucilia illustris* (Meigen), as an indicator of human post-mortem interval: a case of homicide from Fort Lewis, Washington. *Bull. Soc. Vector Ecol.* 11:271-75
81. Lord, W. D., Johnson, R. W., Johnson, F. 1986. The blue bottle fly, *Calliphora vicina* (= *erythrocephala*) as an indicator of human post-mortem interval: a case of homicide from suburban Washington, D. C. *Bull. Soc. Vector Ecol.* 11:276-80
82. Lord, W. D., Rodriguez, W. C. 1989. Forensic entomology: the use of insects in the investigation of homicide and untimely death. *Prosecutor* 22:41-48
83. Lord, W. D., Stevenson, J. R. 1986. *Directory of Forensic Entomologists*. Washington DC: Am. Reg. Prof. Entomol. 42 pp. 2nd ed.
84. MacLeod, J., Donnelly, J. 1963. Dis-

- persal and interdispersal of blowfly populations. *J. Anim. Ecol.* 32:1-32
85. Mann, R. W., Bass, W. M., Meadows, L. 1990. Time since death and decomposition of the human body: variables and observations in case and experimental field studies. *J. Forensic Sci.* 35:103-11
86. Marchenko, M. I. 1980. Classifying of cadaveric entomofauna. Flies' biology: the forensic medical role. *Sud. Med. Ekspert.* 23:17-20 (In Russian with English abstract)
87. Marchenko, M. I. 1985. Peculiarities of the development of *Chrysomya albiceps* WD (Diptera, Calliphoridae). *Rev. Entomol.* 64:79-84 (In Russian)
88. Marchenko, M. I. 1988. The use of temperature parameters of fly growth in medicolegal practice. General trends. *Proc. Int. Conf. Med. Vet. Dipterol. Ceske Budejovica* 1988:254-57
89. Marchenko, M. I. 1989. Method of retrospective determination of insect development onset in a cadaver. *Sud. Med. Ekspert.* 32:17-20 (In Russian with English summary)
90. Marchenko, M. I., Vinogradova, E. B. 1984. The influence of seasonal temperature changes on the rate of cadaver destruction by fly larvae. *Sud. Med. Ekspert.* 27:11-14 (In Russian with English summary)
91. McKnight, B. E., transl. 1981. *The Washing Away of Wrongs: Forensic Medicine in Thirteenth-Century China*. Ann Arbor: Univ. Michigan. 181 pp. (From Chinese)
92. Meek, C. L., Andis, M. D., Andrews, C. S. 1983. Role of the entomologist in forensic pathology, including a selected bibliography. *Bibliogr. Entomol. Soc. Am.* 1:1-10
93. Megnin, J. P. 1887. La faune des tombeaux. *C. R. Acad. Sci. Paris* 105:948-51
94. Megnin, J. P. 1894. La faune des cadavres: application de l'entomologie a la medecine legale. *Encyclopedie Scientifique des Aides-Memoires*. Paris: Masson et Gauthiers-Villars. 214 pp.
95. Micozzi, M. S. 1986. Experimental study of postmortem change under field conditions: effects of freezing, thawing, and mechanical injury. *J. Forensic Sci.* 31:953-61
96. Nabaglo, L. 1973. Participation of invertebrates in the decomposition of rodent carcasses in forest ecosystems. *Ekol. Pol.* 21:251-70
97. Nainis, I. V. J., Marchenko, M. I., Kazak, A. N. 1982. A calculation method for estimating by entomofauna the period during which the body had remained in the place where it was found. *Sud. Med. Ekspert.* 25:21-23 (In Russian with English abstract)
98. Nishida, K. 1982. Experimental studies on the estimation of post mortem intervals by means of flies infesting human cadavers. *Jpn. J. Leg. Med.* 38:24-41
99. Nishida, K., Shinonaga, S., Kano, R. 1986. Growth tables of fly larvae for the estimation of post mortem intervals. *Ochanomizu Med. J.* 34:9-24
100. Nuorteva, P. 1987. Empty puparia of *Phormia terraenovae* R.-D. (Diptera, Calliphoridae) as forensic indicators. *Ann. Entomol. Fenn.* 53:53-56
101. Deleted in proof
102. Nuorteva, P., Hasanen, E. 1972. Transfer of mercury from fishes to in sarcosaprophagous flies. *Ann. Zool. Fenn.* 9:23-27
103. Nuorteva, P., Nuorteva, S. 1982. The fate of mercury in sarcosaprophagous flies and in insects eating them. *Ambio* 11:34-37
104. Payne, J. A. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology* 46:592-602
105. Prichard, J. G., Kossoris, P. D., Leibovitch, R. A., Robertson, L. D., Lovell, W. F. 1986. Implications of trombiculid mite bites: report of a case and submission of evidence in a murder trial. *J. Forensic Sci.* 31:301-6
106. Reed, H. B. 1958. A study of dog carcass communities in Tennessee, with special reference to the insects. *Am. Midl. Nat.* 59:213-45
107. Reiter, C. 1984. Zum Wachstumsverhalten der Maden der blauen Schmeissfliege *Calliphora vicina*. *Z. Rechtsmed.* 91:295-308
108. Reiter, C., Wollenek, G. 1982. Bemerkungen zur Morphologie forensisch bedeutsamer Fliegenmaden. *Z. Rechtsmed.* 89:197-206
109. Reiter, C., Wollenek, G. 1983. Zur Artbestimmung der Maden forensisch bedeutsamer Schmeissfliegen. *Z. Rechtsmed.* 90:309-16
110. Reiter, C., Wollenek, G. 1983. Zur Artbestimmung der Puparien forensisch bedeutsamer Schmeissfliegen. *Z. Rechtsmed.* 91:61-69
111. Rodriguez, W. C., Bass, W. M. 1983. Insect activity and its relationship to decay rates of human cadavers in east Tennessee. *J. Forensic Sci.* 28:423-32
112. Rodriguez, W. C., Bass, W. M. 1985. Decomposition of buried bodies and methods that may aid in their location. *J. Forensic Sci.* 30:836-52
113. Schoenly, K., Reid, W. 1983. Commu-

- nity structure of carrion arthropods in the Chihuahuan desert. *J. Arid Environ.* 6:253-63
114. Schoenly, K., Reid, W. 1987. Dynamics of heterotrophic succession in carrion arthropod assemblages: discrete series or a continuum of change? *Oecologia (Berlin)* 73:192-202
115. Smeeton, W. M. I., Koelmeyer, T. D., Holloway, B. A., Singh, P. 1984. Insects associated with exposed human corpses in Auckland, New Zealand. *Med. Sci. Law* 24:167
116. Smith, K. G. V. 1986. *A Manual of Forensic Entomology*. London: British Museum (Natural History), Comstock. 205 pp.
117. Thomas, D. B., Chen, A. C. 1989. Age determination in adult screw-worms (Diptera: Calliphoridae) by pteridine levels. *J. Econ. Entomol.* 82:1140-44
118. Tullis, K., Goff, M. L. 1987. Arthropod succession in exposed carrion in a tropical rainforest on Oahu, Hawaii. *J. Med. Entomol.* 24:332-39
119. Tyndale-Biscoe, M., Kitching, R. L. 1974. Cuticular bands as age criteria in the sheep blowfly *Lucilia cuprina*. *Bull. Entomol. Res.* 64:161-74
120. Vincent, C., McE Kevan, D. K., Leclercq, M., Meek, C. L. 1985. A bibliography of forensic entomology. *J. Med. Entomol.* 22:212-19
121. Vinogradova, E. B., Marchenko, M. I. 1984. The use of temperature parameters of fly growth in the medicolegal practice. *Sud. Med. Ekspert.* 27:16-19
122. Wall, R., Langley, P. A., Stevens, J., Clarke, G. M. 1990. Age determination in the old-world screw-worm fly *Chrysomya bezziana* by pteridine fluorescence. *J. Insect Physiol.* 36:213-18
123. Webb, J. P. Jr., Loomis, R. B., Madon, M. B., Bennett, S. G., Green, G. E. 1983. The chigger species *Eutrombicula belkini* Gould (Acari: Trombiculidae) as a forensic tool in a homicide investigation in Ventura County, California. *Bull. Soc. Vector Ecol.* 8:141-46
124. Williams, H. 1984. A model for aging of fly larvae in forensic entomology. *Forensic Sci. Int.* 25:191-99
125. Williams, H., Richardson, A. M. M. 1984. Growth energetics in relation to temperature for larvae of four species of necrophagous flies (Diptera: Calliphoridae). *Aust. J. Ecol.* 9:141-52



CONTENTS

THE ANALYSIS OF PARASITE TRANSMISSION BY BLOODSUCKING INSECTS, <i>Christopher Dye</i>	1
HOST-SEEKING BEHAVIOR AND MANAGEMENT OF TSETSE, <i>John Colvin and Gabriella Gibson</i>	21
SMALL ERMINE MOTHS (<i>YPONOMEUTA</i>): Their Host Relations and Evolution, <i>Steph B. J. Menken, W. M. Herrebout, and J. T. Wiebes</i>	41
THE CHEMICAL ECOLOGY OF APHIDS, <i>J. A. Pickett, L. J. Wadhams, C. M. Woodcock, and J. Hardie</i>	67
TACTICS FOR MANAGING PESTICIDE RESISTANCE IN ARTHROPODS: Theory and Practice, <i>I. Denholm and M. W. Rowland</i>	91
FUNCTIONAL MORPHOLOGY OF INSECT WINGS, <i>Robin J. Wootton</i>	113
ECOLOGY OF INFOCHEMICAL USE BY NATURAL ENEMIES IN A TRITROPHIC CONTEXT, <i>Louise E. M. Vet and Marcel Dicke</i>	141
THE BIOLOGY AND MANAGEMENT OF AFRICANIZED HONEY BEES, <i>Mark L. Winston</i>	173
IRON ECONOMY IN INSECTS: Transport, Metabolism, and Storage, <i>Michael Locke and H. Nichol</i>	195
ACCUMULATION OF YOLK PROTEINS IN INSECT OOCYTES, <i>Alexander S. Raikhel and Tarlochan S. Dhadialla</i>	217
FORENSIC ENTOMOLOGY IN CRIMINAL INVESTIGATIONS, <i>E. P. Catts and M. L. Goff</i>	253
INSECT CUTICLE SCLEROTIZATION, <i>Theodore L. Hopkins and Karl J. Kramer</i>	273
MATURATION OF THE MALE REPRODUCTIVE SYSTEM AND ITS ENDOCRINE REGULATION, <i>George M. Happ</i>	303
THE EVOLUTION OF APHID LIFE CYCLES, <i>Nancy A. Moran</i>	321
FEEDING BEHAVIOR, NATURAL FOOD, AND NUTRITIONAL RELATIONSHIPS OF LARVAL MOSQUITOES, <i>R. W. Merritt, R. H. Dadd, and E. D. Walker</i>	349

FRUGIVORY, SEED PREDATION, AND INSECT-VERTEBRATE INTERACTIONS, <i>R. Sallabanks and S. P. Courtney</i>	377
POLYDNAVIRUSES: Mutualists and Pathogens, <i>Jo-Ann G. W. Fleming</i>	401
SAMPLING INSECT POPULATIONS FOR THE PURPOSE OF IPM DECISION MAKING, <i>M. R. Binns and J. P. Nyrop</i>	427
NONLINEAR DYNAMICS AND CHAOS IN INSECT POPULATIONS, <i>J. A. Logan and J. C. Allen</i>	455
ROLE OF ANTS IN PEST MANAGEMENT, <i>M. J. Way and K. C. Khoo</i>	479
ODOR PLUMES AND HOW INSECTS USE THEM, <i>John Murlis, Joseph S. Elkinton, and Ring T. Cardé</i>	505
THE COST OF MIGRATION IN INSECTS, <i>M. A. Rankin and J. C. A. Burchsted</i>	533
ADVANCES IN IMPLEMENTING INTEGRATED PEST MANAGEMENT FOR WOODY LANDSCAPE PLANTS, <i>M. J. Raupp, C. S. Koehler, and J. A. Davidson</i>	561
LIFE-TABLE CONSTRUCTION AND ANALYSIS IN THE EVALUATION OF NATURAL ENEMIES, <i>T. S. Bellows, Jr., R. G. Van Driesche, and J. S. Elkinton</i>	587
THE MODE OF ACTION OF <i>BACILLUS THURINGIENSIS</i> ENDOTOXINS, <i>Sarjeet S. Gill, Elizabeth A. Cowles, and Patricia V. Pietrantonio</i>	615
REGULATION OF DIVISION OF LABOR IN INSECTS SOCIETIES, <i>Gene E. Robinson</i>	637
INDEXES	
Subject Index	667
Cumulative Index of Contributing Authors, Volumes 28–37	676
Cumulative Index of Chapter Titles, Volumes 28–37	679